

Catalogue of American Amphibians and Reptiles.

ANDERSON, JAMES D. 1967. *Ambystoma maculatum*.

***Ambystoma maculatum* (Shaw)
Spotted salamander**

Lacerta maculata Shaw, 1802, Gen. Zool., 3, pt. 1, p. 304. Type-locality, "Carolina," restricted to "vicinity of Charleston, South Carolina" by Schmidt (1953:20). Type not known to exist; collector unknown.

Ambystoma maculatum: Stejneger, 1902:239.

Lacerta punctata Linnaeus, 1766:370 (not of Linnaeus, 1758).

Ambystoma punctata: Baird, 1849:283.

Ambystoma punctatum: Cope, 1867:175.

Salamandra palustris Bechstein, 1800:544 (not of Schneider, 1799). Substitute name.

Salamandra venenosa Daudin, 1803:229. Type-locality, "Philadelphia [Philadelphia Co., Penna.] . . . à peu de distance de cette ville." Type not known to exist. See Nomenclatural History.

Lacerta subviolacea Barton, 1804:109. Type-locality, "a few miles from the city of Philadelphia [Philadelphia Co., Penna.]." Type not known to exist. See Nomenclatural History.

Ambystoma carolinae Gray, 1850:35. See Nomenclatural History.

Ambystome argus Duméril, Bibron and Duméril, 1854:103. Lapsus for *Ambystoma*; substitute name. See Nomenclatural History.

Salamandra margaritifera ms. Mus. Paris, *vide* Duméril, Bibron and Duméril (*op. cit.*:105). See Nomenclatural History.

• CONTENT. No subspecies have been recognized.

• DEFINITION. A stout-bodied *Ambystoma* ranging to almost 230 mm in total length (most adults exceeding 165 mm), *A. maculatum* is characterized by a dark dorsum with two irregular rows of round spots on either side of the mid-dorsal line. The spots begin on the head near the eyes and extend to the tip of the tail. The dark ground color is usually black, blue-black, or slate although rare individuals are dark brown. In life the spots are usually bright yellow but are occasionally almost cream color. The first pair of spots is sometimes orange. Unspotted individuals are rare but probably occur throughout the range. The ventral surface is slate-gray in life but is subject to ontogenetic and seasonal variation, being lighter in sub-adults and slightly paler in females during the breeding season. The usual number of costal grooves is 12 although 11 and 13 are frequent variations. The teeth are in single rows. Lingual plicae radiate from the posterior part of the tongue.

The larvae are of the pond type (Valentine and Dennis, 1964), and retain balancers until a total length of 15–20 mm is attained. In general, the larvae of *A. maculatum* appear more slender and less robust than those of most eastern species, and the tail fin is not as deep. The coloration is nondescript: the pigment is uniformly dispersed except for an ill-defined variable pigment-free lateral line. The ventral surface is essentially free of melanophores.

• DESCRIPTIONS. Numerous brief descriptions of eggs and egg masses from the field are scattered throughout the herpetological literature. The most useful references have been given by Wright (1908), B. G. Smith (1911), Brimley (1921), Breder (1927), and Bishop (1941; 1947). Bishop (1941) gave detailed information and a useful guide to the literature. Egg capsules were described by Piersol (1929), von Wahlert (1953), and Salthe (1963). Gilbert (1942) described the relationship of egg capsules and the green alga *Oophila amblystomatis*.

Since *maculatum* has been widely used in experimental embryology (often under the name *Ambystoma punctatum*), there are numerous references and specialized descriptions in that literature. Eycleshymer (1895), Rugh (1962), and Nelsen (1953) listed useful references, including bibliographies, dealing with cleavage and developmental stages.

Spermatophores have been described by Wright and Allen (1909), Smith (1910), and Bishop (1941; 1947). B. G. Smith (1910) also described the spermatozoa.

Brief descriptions of the larvae are scattered through the literature; many specialized descriptions occur in the em-

bryological literature. For identification and taxonomic purposes the best are found in works by B. G. Smith (1911), Dunn (1918), Bishop (1941; 1947), and Brandon (1961). Rugh (1962) illustrated the Harrison (unpublished) stages of development from uncleaved eggs to hatched larvae.

Adults have been described in numerous regional guides and keys; the best diagnostic descriptions are found in works by Cope (1867; 1889), H. M. Smith (1934), Bishop (1941; 1947), and P. W. Smith (1961). The hyoid apparatus was described by Cope (1887); the opercular apparatus by Monath (1965); the general features of the skull by Hoheisel (1931); details of cranial morphology by Theron (1952); certain features of the osteology by Tihen (1958) and Stokely and Holle, 1953, 1954; the cloaca and oviduct by von Wahlert (1953); the spermatheca by Noble (1931); and the male urogenital system by Baker and Taylor (1964), Noble (1931), Nelsen (1953), and von Wahlert (1953).

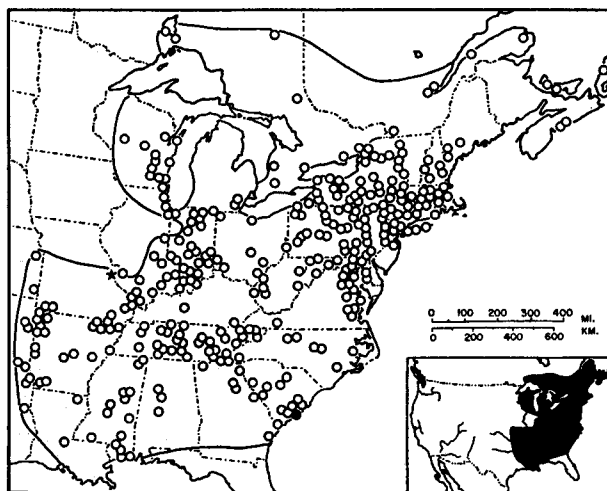
Wonderly (1963) described the gross anatomy of the digestive system and provided data on the relative length of organs compared to other salamanders. The histology of the digestive tract was studied by Bates (1904).

Piatt (1938) described the development of the individual cranial muscles. The musculature and vascularization of normal and regenerated limbs was described by I. Blount (1935).

• ILLUSTRATIONS. This common species is frequently illustrated. The following references are considered important and accessible; the list is by no means exhaustive.

Spermatophores were figured by B. G. Smith (1910) and Bishop (1941; 1947). Eggs were illustrated by Eycleshymer (1895), Rugh (1962: developmental stages), Nelsen (1953: cleavage), Anon. (1953: developmental stages). The egg mass is frequently illustrated; see Bishop (1941) for photographs and additional references. Salthe (1963) illustrated the jelly mass and egg capsules.

Larvae were illustrated by Cope (1889), B. G. Smith (1911), Bishop (1941; 1947), Brandon (1961), and Rugh (1962: the unpublished Harrison stages). R. F. Blount (1932) provided a color plate illustrating normal larval pigmentation and showing the effects of pituitary extirpation and transplantation on larval pigmentation. Illustrations of adults are numerous; the best recent photographs and drawings are available in works by Bishop (1941; 1947), H. M. Smith (1956), Conant (1958), and P. W. Smith (1961). Cope (1889) figured many structures of *A. maculatum* including skeleton, skull, hyoid apparatus, and visceral anatomy. The tongue and arrangement of teeth were illustrated by Bishop (1941), and tooth structure and certain features of osteology by Tihen (1958). Baker and Taylor (1964) illustrated the male urogenital system. Hilton (1962) illustrated the superficial and deep muscles of the shoulder region. Breder (1927) and Noble (1931) diagrammed courtship activities. Piatt (1938) illustrated transverse and sagittal sections of larval crania showing the morphogenesis of cranial



MAP. The solid symbol marks the type-locality; open circles indicate other localities. The star indicates a fossil locality.

muscles. I. Blount (1935) illustrated the musculature of normal and reduplicated limbs. Wonderly (1963) provided drawings of the digestive system.

• **DISTRIBUTION.** The spotted salamander is known from Nova Scotia, Prince Edward Island, and mainland New Brunswick west to central Ontario and south to the Gulf Coast. On the western periphery of the range it is known from eastern and central Wisconsin, the forested parts of Illinois (not the Grand Prairie region), the southern two-thirds of Missouri, extreme southeastern Kansas, eastern Oklahoma and Texas. In the past range maps have shown gaps in the distribution, especially in the mid-south (Bishop, 1947). Recent reports, however, indicate no natural breaks in the distribution (Gentry, 1955; Green, 1956) through the central parts of the range. Additional locality records from the mid-south, especially Kentucky, are needed as are local distributional studies from any part of the range. The least known areas are the southern and southeastern parts of the range, especially the coastal plain. Neill (1954) discussed the distribution in the southeast, but numerous locality records are required before the precise limits of distribution in this area are known.

This species seems to be restricted to hardwood and mixed deciduous forest situations that have temporary or semi-permanent ponds available for breeding. It may be absent from areas in which ponds are flooded by streams or rivers and is usually absent where permanent fish populations occur.

The larvae of *A. maculatum* often share ponds with the larvae of one or more other species of *Ambystoma*. Although the ecological relations between the species are not well known, certain interactions between larval *maculatum* and other species of *Ambystoma* have been discussed by Anderson and Graham (1967). In parts of the range *A. maculatum* may be prevented from using certain ponds by the presence of larval *A. tigrinum*. The larvae of the two species occur sympatrically on Long Island, New York (S. Yeaton, pers. comm.), but no other authenticated records are known.

For literature records of specific localities in addition to those cited below for breeding dates, see papers by Black and Dellinger (1938, Arkansas), Dowling (1957, Arkansas), Babbitt (1937, Connecticut), Martof (1955, Georgia), P. W. Smith (1961, Illinois), P. W. Smith and Minton (1957, Indiana and Illinois), Hall and Smith (1947, Kansas), Barbour (1953, Kentucky), Cook (1957, Mississippi), Siebert and Brandon (1960, Ohio), Bragg and Hudson (1951, Oklahoma), Parker (1947, Tennessee), Gentry (1955, Tennessee), Burt (1938, Texas), H. M. Smith and Sanders (1952, Texas), Suzuki (1951, Wisconsin), and Neill (1954, southeast). Distributional records in Canada were summarized by Bleakney (1958) and by Logier and Toner (1961).

• **FOSSIL RECORD.** Holman (1965) recorded this species from a late Pleistocene cave deposit near St. Louis, Missouri, on the basis of a single body vertebra.

• **PERTINENT LITERATURE.** Relationships and phylogeny were discussed by Cope (1867; 1889), Noble (1931), and Tihen (1958). Stejneger (1902) gave a comprehensive synonymy for *A. maculatum*.

The courtship was described by Breder (1927), and Bishop (1941); Noble (1931) discussed the phylogenetic significance of courtship behavior. Breeding migrations were described and analyzed by Wright (1908), Blanchard (1930), Bishop (1941), Baldauf (1952), and Peckham and Dineen (1955). Whitford and Vinegar (1966) described homing behavior, and Shoop (1965) discussed orientation with respect to movements to and from breeding ponds. Murphy (1962) studied movements of adults and juveniles. Some aspects of population dynamics were discussed by Husting (1965). Collecting techniques and rearing of larvae in the laboratory were discussed by Moulton (1954); Dempster (1930) described the growth of larvae under natural conditions. Bishop (1941) summarized information on the life cycle and natural history. Bleakney (1952), and Whitford and Vinegar (1966) reported overwintering of larvae. Records of albinism in this species were summarized by Hensley (1959).

Breeding dates for various parts of the range have been given by Bishop (1941, New York), Blanchard (1930, Michigan), Baldauf (1952, Pennsylvania), Brimley (1921, North Carolina), Wood and Wilkinson (1952, Virginia), Peckham and Dineen (1955, Indiana), Green (1956, West Virginia), Gentry (1955, Tennessee), Huheey and Stupka (1965, Tennessee), and Bragg (1955, Oklahoma).

The symbiotic relationship between *A. maculatum* embryos and the alga *Oophila amblystomatis* was described and dis-

cussed by Gilbert (1942; 1944), Hutchison and Hammen (1958), and Hammen and Hutchison (1962). Cliburn and Ward (1963) summarized the geographic localities from which this alga-egg association has been reported.

Hutchison (1961) presented some information on the temperature tolerances of adults; Moore (1939) discussed the developmental rate of eggs. Whitford and Hutchison (1963, 1965, 1966) discussed cutaneous and pulmonary gas exchange in adults and later (1967) correlated oxygen consumption with the ratio of body weight to respiratory surface and compared *A. maculatum* with other species. Helff (1927) studied oxygen consumption in larvae. Relevant information and references on metabolism, blood and respiration, water balance and kidney function, metamorphosis, developmental physiology and regeneration are summarized by various contributors in "Physiology of the Amphibia" edited by Moore (1964).

Etkin (1955) discussed the pituitary-thyroid relationships during metamorphosis, and Etkin and Sussman (1961) reported the necessity of hypothalamic intervention for metamorphosis. The development and responses of isolated melanophores in tissue culture have been studied by Twitty and Bodenstein (1939), Wilde (1955) and Novales and Novales (1961).

The effects of extirpation and transplantation of pituitary rudiments upon larval pigmentation, growth, growth rate and proportions were discussed by R. F. Blount (1932; 1935). The influence of diet and low temperature on embryonic growth and limb morphogenesis was studied by I. Blount (1950).

• **NOMENCLATURE HISTORY.** The three oldest names for the spotted salamander were based on the illustration in Catesby's "Natural History of the Carolinas" (1731-1743). In the twelfth edition of "Systema Naturae," Linnaeus (1766) used *Lacerta punctata* for this species, although previously (1758) he had used that name for a lizard. The name *palustris* was in use for a European salamander before Bechstein (1800) proposed it for the spotted salamander. Shaw's name *maculatum* is therefore the oldest available for the species.

Barton described *Lacerta subviolacea* in an address before the American Philosophical Society in 1803. Prior to publication of the Transactions of the society in 1804, Daudin named *Salamandra venenosa*, based on Barton's description which he obtained in a letter from Rafinesque (Daudin, 1803). Therefore both names apply to the same specimen.

Gray (1850) used the name *Ambystoma carolinae* for *A. maculatum*. This is apparently the first use of the name *carolinae*, since Gray's citation of *Lacerta carolinae* Linnaeus 1758 appears to be in error.

Duméril, Bibron and Duméril (1854) proposed *Ambystome argus* as a substitute name for all pre-existing names. The same authors mentioned that the name *Salamandra margaritifera* had been applied to specimens of *A. maculatum* in the Museum of Natural History, Paris.

• **ETYMOLOGY.** The name *maculatum* (Latin *maculatus*, spotted) refers to the spotted coloration of this species.

COMMENT

Although this species is reasonably well known for an *Ambystoma*, there is great need for studies on local distribution, especially in the southern parts of the range. Larval ecology, variations in larval characters and variations in the life history are very poorly known.

Geographic variation has not been adequately studied. P. W. Smith (1961) found considerable geographic variation within Illinois and suggested that strong geographic trends might exist throughout the range of the species.

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